Dispatches

Cephalopod Behaviour: Skin Flicks

Cephalopods, such as octopus and squid, can change their coloration in an instant, and even produce moving patterns on their skin. A new study describes these wavelike patterns in a colourful tropical cuttlefish, providing insights into the neural mechanisms that generate them.

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Before the dismal rise of model organisms, comparative physiology flourished under the banner of Krogh's principle, which states that for each problem there is an ideal organism. The squid giant axon is an excellent example. Another type of cephalopod mollusc, the flamboyant cuttlefish, *Metasepia tullbergi*, is now emerging as the organism of choice for the study of moving patterns on the skin, as illustrated by the work reported by Laan *et al.* [1] in this issue of *Current Biology*. Like most cephalopods, cuttlefish can change their appearance with remarkable flexibility and speed (Figure 1A); while sometimes cryptic, as their name suggests, flamboyant cuttlefish can also display bright colours, which may warn potential predators that they are toxic [2]. Adding to the dramatic effect, *Metasepia* displays dark moving bands [1] known as 'passing cloud' patterns, which are familiar in octopuses, cuttlefishes and squid [3,4] (use the YouTube search terms 'passing cloud' and 'cuttlefish' or 'octopus'), but have been difficult to study in laboratory aquaria. *Metasepia* uses the patterns frequently, and they are unusually complex, giving insights into the mechanisms that generate the waves.

Cephalopod skin is a remarkable organ (Figure 1B), both in the way that it combines different optical elements — three layers of chromatophores, mirror-like iridophores, and matte white leucophores — and, as Messenger [5] says, as "a unique motor system that operates upon the environment without applying force to it". Coloration changes are produced by the neurally driven chromatophores [5]. Each chromatophore cell contains an elastic sac. This is opened by the muscles attached to the cell to form a coloured patch about 300 μm across, but collapses when relaxed to reveal the underlying light tissue. Chromatophores have an overall density of about 50 per mm^2. Chromatophore muscles are innervated by up to six excitatory motor neurons, which may allow them to contribute to different coloration patterns (Figure 1A). Each motor neuron innervates a patch of about ten chromatophores [5]. In the absence of neural input, cephalopod skin spontaneously generates poetically named 'wandering clouds', dark bands that move across the skin which may be due to electrical coupling of the chromatophore muscles [5] (Figure 1 dotted lines), and are clearly related to the passing cloud display.

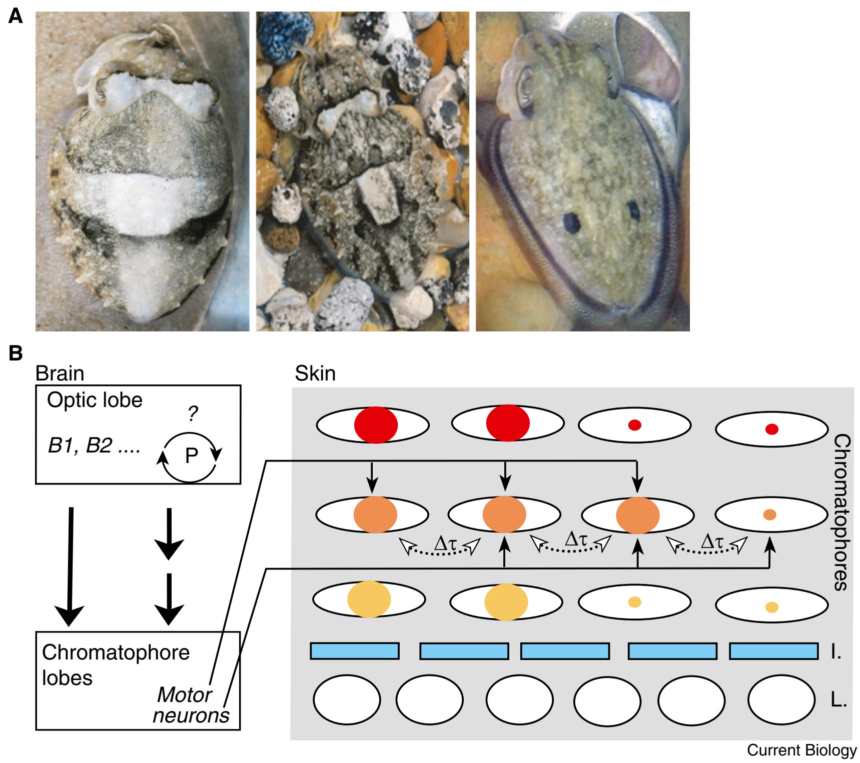

Figure 1. Coloration patterns of the cuttlefish *Sepia officinalis*, and the mechanisms used to produce them.

(A) Two camouflage patterns, left and centre, and a deimatic pattern used to deter approaching predators [6,7]. (B) Diagram of cephalopod skin and two of the brain structures controlling coloration [1,5]. The skin has three layers of chromatophores, each with a different type of coloured pigment, above a layer of iridophores (I.), which contain multi-layered mirror-like reflective elements that produce structural colours — and are important in polarisation signalling. Finally the leucophores (L.) contain a diffuse white pigment which forms a background for the chromatophore colours. Dotted lines represent hypothetical electrical connections with temporal delays (Δτ) between chromatophore muscles that in the absence of neural input produce wandering cloud patterns. In the brain the optic lobes are important in producing co-ordinating movements and controlling the expression of the main body patterns (*B1, B2* ....) [3,5,6], which suggests that they might contain pacemakers (P) involved in travelling wave patterns [1]. The optic lobes connect via direct and indirect pathways to the chromatophore lobes, which contain the chromatophore motor neurons. (Images in (A) courtesy of S. Zylinski and K. Langridge.)

Passing clouds move over static coloration patterns (Figure 1A). The basic components of these patterns include local light and dark features, such as lines, squares and spots, as well as more global mottles and stipples [3]. The European cuttlefish has about 35 such components, while *Metasepia pfefferi* has about 17 [5]. The expression of chromatic components is co-ordinated to produce about a dozen body patterns, which are used for camouflage and communication [3,6–8]. Much as human faces can combine our basic expressions of emotion, for example happiness and surprise, or fear and disgust, body patterns can be combined with great potential for versatility, allowing subtlety in camouflage design and visual signalling.

Within this repertoire of patterns, the passing clouds are fascinating and enigmatic. They appear in all the main cephalopod groups: squid, cuttlefish and octopus, often with wavelength comparable to the body length and a frequency of about 1 Hz, moving either forwards or backwards. Their function is not clear: they are sometimes used when hunting, and it has been suggested that they may 'hypnotise prey' [4]. European cuttlefish use passing clouds when swimming, and although they are conspicuous they may prevent predators from judging the animal's velocity, like an enhanced version of military 'dazzle' patterns [9]. *Metasepia tullbergi* has an exceptionally complex display, the dark bands pass over four contiguous regions on each side of the body, each with a separate point of origin. When they are expressed in more than one region the waves are synchronised. The waves can move at a ten-fold range of speeds but keep a constant wavelength, which means that one band is normally visible in each region at any time. The waves can also 'blink', transiently disappearing from a patch of skin. These observations suggested that the 'passing clouds' are generated by central pacemakers, rather than (or perhaps in addition to) the myogenic waves that generate 'wandering clouds' [1,5] (Figure 1B).

Interestingly, Laan *et al.* [1] argue that the waves may be related to more conventional oscillatory movements, such as those used for swimming. This ties nicely with the finding that localised electrical stimulation of the optic lobes of the cephalopod brain (Figure 1B) can cause the animals to express familiar body patterns or to produce locomotor behaviour [5]. By comparison, the chromatophore lobes, which lie downstream of the optic lobes and contain the chromatophore motor neurons, seem a less likely centre for wave generation, because they seem to lack a somatotopic organization — neighbouring motor neurons do not project to neighbouring points on the body — which would allow them to propagate travelling waves across the skin [5].

A special appeal of cephalopods is that they are perhaps the nearest we will get to intelligent life from another planet. They have independently evolved vertebrate-like complexity, doing some things much like fish — or ourselves — and others very differently. What little is known offers much promise in the understanding of chance and necessity in brain evolution.

References

1. Laan, A., Gutnick, T., Kuba, M.J., and Laurent, G. (2014). Behavioral analysis of cuttlefish traveling waves and its implications for neural control. Curr. Biol. *24*, 1737–1742.
2. Williams, B.L., Hanifin, C.T., Brodie, E.D., and Caldwell, R.L. (2011). Ontogeny of tetrodotoxin levels in blue-ringed octopuses: maternal investment and apparent independent production in offspring of *Hapalochlaena lunulata*. J. Chem. Ecol. *37*, 10–17.
3. Hanlon, R.T., and Messenger, J.B. (1988). Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): The morphology and development of body patterns and their relation to behaviour. Phil. Trans. R. Soc. Lond. B *320*, 437–487.
4. Mather, J.A., and Mather, D.L. (2006). Apparent movement in a visual display: the 'passing cloud' of *Octopus cyanea* (Mollusca: Cephalopoda). J. Zool. *263*, 89–94.
5. Messenger, J.B. (2001). Cephalopod chromatophores: neurobiology and natural history. Biol. Rev. *76*, 473–528.
6. Hanlon, R.T. (2007). Cephalopod dynamic camouflage. Curr. Biol. *17*, 400–404.
7. Langridge, K.V., Broom, M., and Osorio, D. (2007). Selective signalling by cuttlefish to predators. Curr. Biol. *17*, R1044–R1045.
8. Zylinski, S., Osorio, D., and Shohet, A.J. (2009). Perception of edges and visual texture in the camouflage of the common cuttlefish, *Sepia officinalis*. Phil. Trans. R. Soc. B *364*, 439–448.
9. Scott-Samuel, N.E., Baddeley, R., Palmer, C.E., and Cuthill, I.C. (2011). Dazzle camouflage affects speed perception. PLoS ONE *6*, e20233.

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Obesity: Cognitive Impairment and the Failure to 'Eat Right'

A recent study has found that obese women (but not men) have difficulty inhibiting food-rewarded, but not money-rewarded, appetitive behaviour, suggesting that obesity is associated with cognitive deficits that could selectively promote food intake, perhaps in a sex-dependent manner.

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> *"If we could give every individual the right amount of nourishment and exercise, not too little and not too much, we would have found the safest way to health"*
>
> (From Hippocrates (460-377 BC) *Hippocratic Writings*. Chicago: Encyclopedia Britannica, 1955).

The prescription for health offered by Hippocrates more than 2000 years ago continues to be sound advice. Most of us are aware that failing to follow it can result in excess weight gain and increased risk of heart disease, type II diabetes, hypertension, stroke, and cancer. Indeed, it may be difficult to find anyone who doesn't know that they should "Eat right and exercise". Yet we are now in the midst of a global obesity pandemic. An obvious question is why millions of overweight and obese people are unable to eat right (i.e. less)? The findings reported in this issue of *Current Biology* by Zhang *et al.* [1] offer an answer to the question of why eating 'right' has become so difficult.

Zhang *et al.* [1] trained obese and normal weight men and women on two simple discrimination problems with different colored visual cues serving as discriminative stimuli for reward and nonreward. Half of the participants were trained with food rewards and